

Moose *Alces alces* behaviour related to human activity

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Cover: Rock carving of a hunting sequence - a moose hit by a spear.
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Abstract

The spatiotemporal dynamics of human activity requires a better understanding of the ecological effects on wildlife. This thesis focuses on the behavioural response of a harvested species, moose (*Alces alces*), to dynamic human activities e.g. hunting and recreation, and to static influences like roads, using experimental and descriptive approaches. Potentially lethal (*hunting*) and non-lethal (*hiking*, *snowmobiling*) activities provoked short-lived increases in moose movement activity and caused spatial displacement. The data suggests a uniform response towards unexpected disturbance and that moose are sensitive to human proximity. Hunting clearly provoked the strongest response. Moose approached by a hunting dog commonly fled, suggesting adjustments in anti-predator behaviour towards a non-native predator. This may lead to predator facilitation where wolves and human predation co-exist, because the moose's behavioural response towards one predator possibly increases the predation risk by the other. Unexpectedly, *hiking* and motor-driven (*snowmobiling*) recreational activity caused a comparable change in moose behaviour. The short-lived response towards dynamic human activities indicates a rather minor impact on moose total energy budget from a single disturbance. Moose seldom crossed roads, but did increasingly so during migration. Road-crossing sites were aggregated, suggesting well established travel routes and corridors for migratory moose. Moose did not cross roads more often during hunting season. In general, moose little utilized habitats in proximity to roads. Moose-vehicle collisions did not occur where and when moose most commonly cross roads. My results suggest a higher risk to human safety during times of poor visibility and close to urban areas, but not necessarily in the vicinity of forests. For wildlife subject to intensive harvest and sensitive to human proximity, I emphasize the need to include animal behavioural, landscape ecological, political as well as socio-economical aspects for future research concerning human-wildlife interactions. I also recommend future research to combine wildlife movement data from active tracking sensors such as GPS-collars together with collision data to improve conclusions about wildlife movement corridors and traffic risk zones.

Keywords: human impact, recreational activities, hunting, infrastructure, movement behaviour, ungulate, experimental disturbances, GPS location data.

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Für meine Eltern

*If you will tell me why
the fen appears impossible
I then will tell you why
I think that I can get across it
if I try*

Marianne Moore

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Appendix

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I Neumann W, Ericsson G, Dettki H. 2009. The non-impact of hunting on moose *Alces alces* movement, diurnal activity, and activity range. *European Journal of Wildlife Research* **55**, 255–265.
DOI 10.1007/s10344-008-0237-0
- II Neumann W, Ericsson G, Dettki H. Non-naïve moose and their anti-predator behaviour towards humans. (manuscript)
- III Neumann W, Ericsson G, Dettki H. The impact of human recreational activities on wildlife – moose as a case study. (manuscript)
- IV Neumann W, Ericsson G, Dettki H, Bunnefeld N, Keuler N, Helmers D, Radeloff VC. Spatial and temporal probability for wildlife road crossings – migratory moose as a model system. (manuscript)

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Introduction

Humans are part of most wildlife habitats. The spatial structure and dynamic nature of human activity needs a better understanding of the ecological effects on wildlife. To preserve wildlife populations, we need to incorporate corresponding knowledge into natural resource management and landscape planning. This is particularly needed when humans are the major source of wildlife mortality by being either the exclusive or an additive top predator. Humans can affect wildlife on different trophic levels. Changes in animal behaviour with respect to human presence can result in complex indirect effects of human activity in ecological systems.

This thesis aims to improve our understanding of the behavioural response of a hunted species, moose (*Alces alces* Linnaeus 1758), to different types of human activities such as hunting, recreation and infrastructure, i.e. roads, using a combination of descriptive and experimental approaches.

Anti-predator behaviour

Anti-predator behaviour theory describes the interplay between prey and predator. Anti-predator behaviour is an evolutionary game, where prey act to minimize predation risk, to avoid detection, making capture less likely, and to prevent consumption (Alcock, 1993). Within this interplay, predator and prey reciprocally affect their distribution in space and time (Luttbeg and Sih, 2004; Brown and Kotler, 2007). In particular, top predators influence prey behaviour and distribution, resulting in trophic cascades which can modify entire ecosystems (Creel *et al.*, 2005; Preisser *et al.*, 2005; Ale and Whelan, 2008; Kittle *et al.*, 2008). For example, being a keystone species in the ecosystem, the reintroduction of wolves (*Canis lupus* Linnaeus 1758)

largely changed the ecosystem structure by increasing the plant diversity and density and enabling the recovery of the beaver (*Castor canadensis* Kuhl 1820) population induced by predation-risk sensitive foraging in the present elk (*Cervus elaphus* Linnaeus 1758) population (Ripple and Beschta, 2004).

Anti-predator behaviour includes trade-off situations with prey altering time allocation between directly and indirectly fitness enhancing activities such as foraging and vigilance. Anti-predator behaviour is complex and is influenced by the characteristics of prey, predator, and environment (Stankowich and Blumstein, 2005; Liley and Creel, 2008). Because of anti-predator behaviour, prey mortality rate is rarely a linear function of predator density (Abrams, 1993). Being a process of decision-making that includes trade-offs, anti-predator behaviour is costly. It can exceed the fitness loss of direct predation and may occur even when predation rate is zero (Lima, 1998; Creel and Christianson, 2007; Peckarsky *et al.*, 2008).

In multi-predator systems, the most abundant predator often shapes prey behavioural response, but response may not necessarily be positively correlated to attack rate (Lima, 1992). Multiple predator effects are non-independent and can result in suboptimal anti-predatory strategies, i.e. predator facilitation, with prey's behavioural response towards one predator increasing the predation risk by the other. For example, gerbils increase their predation risk by owls when adjusting behaviour towards predation by vipers (Kotler *et al.*, 1992; Sih *et al.*, 1998). Alternatively, multiple predator situations can reduce predation risk, resulting in less prey being consumed compared to a single predator situation (Sih *et al.*, 1998; Vance-Chalcraft and Soluk, 2005).

Natural selection should favour risk assessment. Risk of predation varies in space and time, and prey species need to cope with risk of predation adaptively by adjusting their anti-predator strategies accordingly (Lima and Bednekoff, 1999). For example, to minimize their spatiotemporal predation risk by lions (*Panthera leo* Linnaeus 1758), plains zebras (*Equus burchelli* Gray 1824) utilize grassland less during darkness, move faster and in a more tortuous fashion (Fischhoff *et al.*, 2007). Normally, prey have limited information about the actual level of danger and behavioural adjustments follow a learning curve. While an increased risk level often is easy to detect for a prey, a decreased risk is normally more difficult to perceive and often results in a behavioural time lag, as non-optimal trade-offs for example

staying longer than necessary in refuges, and thereby missing foraging or mating opportunities (Sih, 1992; Sih *et al.*, 2000; Welton *et al.*, 2003).

With the exception of situations of extreme starvation or low fitness cost for being wrong, an overestimation of risk is advantageous, compared with the resulting cost of underestimating predation risk (Abrams, 1994). The spatiotemporal variation in predation risk shapes prey organization in space and time, e.g. risk-sensitive foraging, creating a 'landscape of fear' with risky areas being under-utilized, while safe areas being over-utilized (Ripple and Breschta, 2004; Brown and Kotler, 2007). Within this interplay between the predators' and the preys' behaviour, a predator affects the quality of its foraging patch negatively as soon as it arrives (Brown and Kotler, 2007). In turn, changes in prey space use may result in a differential depletion of resources, causing trophic cascades (Creel *et al.*, 2005; Preisser *et al.*, 2005; Berger, 2007). However, responses to predation risk differ among prey species, and may vary with season and environment (Kittle *et al.*, 2008).

Predation risk affects prey demography via altered physiological trade-offs, e.g. elk females reproduce less under high predation risk by wolves (Creel *et al.*, 2007). Such non-consumptive effects by predators on prey may have equal or even greater effect than direct predation, and can affect individual prey performance such as activity, growth, or fecundity negatively and in turn may even influence prey population dynamic negatively (Creel and Christianson, 2007; Peckarsky *et al.*, 2007). The magnitude of the indirect effects of predation is closely correlated to prey competition, resulting in greater impact when prey intra-specific competition is low (Bolnick and Preisser, 2005). Individual body condition further affects the costs of predation and foraging, as individuals in poorer condition face relatively lower costs. They have relatively less to lose and thereby more prone to forage in risky but high productive habitats (Brown and Kotler, 2007). For example, male elk in poorer body condition, showed weaker anti-predator responses than female elk, despite their higher risk of predation by wolves, resulting in wolves over-selecting male elk (Winnie and Creel, 2007).

Humans in wildlife environment

The high spatiotemporal dynamics of human activity needs a better understanding of its ecological consequences. Today, recreational activities cover all seasons (Ingold, 2005). Infrastructure and recreational activities expand gradually into wildlife habitat, increasingly becoming an integral part

of most wildlife species' environments (Knight and Gutzwiller, 1995; Forman and Alexander, 1998; Ingold, 2005; Hawbaker *et al.*, 2008; Stankowich, 2008). Human activity affects wildlife not only directly and indirectly, but can also cause cascading effects. Human activity may also add a level to natural predator-prey systems by affecting the distribution of natural top predators. For example, wolves and bears (*Ursus arctos* Linnaeus 1758) often avoid human proximity, which in turn can attract species of prey like moose and elk in the predator-free space, potentially affecting the vegetation structure (Persson *et al.*, 2000; Hebblewhite *et al.*, 2005; Berger, 2007; Nellemann *et al.*, 2007; Hebblewhite and Merrill, 2008). All in all, the influence of human activity encompasses short- and long-term disturbances, and at both small and large spatial scales. In particular, the combination of short- and long-term disturbances, i.e. infrastructure enables human access into remote areas, may increase disturbance frequencies and may lead to permanent enhanced disturbance levels, potentially affecting wildlife to a greater extent than natural disturbances and risk of predation.

In systems where human harvest dominates or greatly affects wildlife mortality, we expect stronger response to human activity in general. In hunted ungulate populations for example, human-induced disturbances often generate stronger a flight response than in non-hunted populations (Stankowich and Blumstein, 2005; Stankowich, 2008). In this thesis, I define disturbance as a deviation in an animal's behaviour from the patterns occurring without human influences following Frid and Dill (2002). According to the risk-disturbance hypothesis, an animal's response towards human-induced disturbance stimuli should follow the same economic principles used by prey encountering predators with animal responses being stronger when perceived risk is greater (Frid and Dill, 2002).

Human-caused disturbances seem to induce animal responses similar to non-human predation risk, which may cause a re-organization of animals in space creating the 'landscape of fear' (Frid and Dill, 2002; Brown and Kotler, 2007). Yet a failure to relocate in the presence of disturbance does not necessarily reflect a failure to perceive or respond to disturbance, but a lack of alternative habitats to switch to (Gill *et al.*, 2001). Thus, it may be difficult to distinguish correctly whether wildlife have accustomed to human-induced disturbance or if they just do not have any alternative to go to. The inability to relocate to another habitat to avoid human disturbance can be associated with increased levels of stress affecting physiological parameters, which many vary with season (Creel *et al.*, 2002; Barja *et al.*,

2007; Thiel *et al.*, 2008). Furthermore, human-induced disturbance can depress reproductive success, for example, a lower calf-to-female ratio in elk when frequently disturbed by hiking activity during calving season (Phillips and Alldredge, 2000).

Wildlife and hunting activity

Sustained human harvest can strongly affect an ecosystem and drive evolutionary changes in wildlife life history traits with the outcome depending on the management regime (Coltman *et al.*, 2003; Milner *et al.*, 2007; Proaktor *et al.*, 2007; Mysterud *et al.*, 2009). In systems where human harvest, i.e. human predation, accounts for the major source of mortality either as the exclusive, or as an additional top predator, we expect corresponding modifications in prey anti-predator behaviour to reduce the risk of predation by the dominant predator (Lima, 1992; Sand *et al.*, 2006). As a result, human predation may have the capability to structure ecosystems like other top predators do (Ripple and Breschta, 2004). Anti-predatory strategies may have evolved in response to human hunting. This may result in broader ecological consequences with respect to the anti-predator behavioural response to other natural top predators such as re-colonizing wolves, i.e. predator facilitation (Kotler *et al.*, 1992; Sih *et al.*, 1998; Sand *et al.*, 2006). For example, anti-predator behaviour such as grouping and movement activity in elk can be more related to the predation by humans than wolves (Proffitt *et al.*, 2009). Such relationships support the idea of anti-behavioural adaptation towards human predation and the perception of humans as predator in ungulates. Likewise, Theuerkauf and Rouys (2008) suggest that hunting and habitat alteration affected the distribution of red deer (*Cervus elaphus* Linnaeus 1758), roe deer (*Capreolus capreolus* Linnaeus 1758) as well as wild boar (*Sus scrofa* Linnaeus 1758) more than predation risk by wolves does. Apparently, red deer react strongly to hunting pressure (Theuerkauf and Rouys, 2008). Hunting activity causes momentary behavioural changes such as habitat shifts in prey (Millsaugh *et al.*, 2000; Vieira *et al.*, 2001). Beyond temporary behavioural changes and in line with predator-prey theory, we presume behavioural evolutionary modifications to be reasonable in ungulates with respect to human predation. We expect such modifications in particular where prey experienced a long-lived strong harvest pressure persisted with high population turnover, and natural top predator were absent over a long periods such as for Scandinavian moose (Swenson *et al.*, 1994; Solberg *et al.*, 2000; Ericsson and Wallin, 2001; Wabakken *et al.*, 2001).

Many European countries have a long tradition in using dogs (*Canis lupus familiaris* Linnaeus 1758) for hunting game. Apart from popularity, fairly little attention has been given to interactions between hunting dogs and game in the hunting situation from an evolutionary game perspective (but see Sweeney *et al.*, 1971; Cederlund and Kjellander, 1991; Bateson and Bradshaw, 1997; Ericsson, 2001; Baskin *et al.*, 2004). Some studies address also the effect of using a hunting dog on hunting success (Ball *et al.*, 1999; Ruusila and Pesonen, 2004). In Scandinavia, hunting dogs that hold their target game at bay are common when hunting moose, or small game (Thelander, 1992; Lavsumund *et al.*, 2003). To address ungulate, e.g. moose, behavioural response towards their current major source of mortality, it is important to choose an area where the presence of wolves has been negligible for several decades, but where human harvest has replaced natural predation for a long time (Ericsson and Wallin, 2001), as given in the study area of this thesis. Hunting regulations and traditions differ between North America and Northern Europe (Heberlein, 2000). Thus, public and private land are less distinctive in Sweden with respect to hunting activity compared to North America, precluding the access of hunting impact corresponding to animal movement into refuges.

To access the impact of different hunting activity in an ungulate population subject to sustained hunting pressure, I evaluated individual moose movement activity among periods of different hunting activity on a large spatiotemporal level. For this purpose, I analyzed moose from three areas of differential hunting pressure and human presence (Paper I). Secondly, to access specifically the behavioural response to moose hunt on the individual level and on a finer spatiotemporal scale, I analyzed moose movement, space use and behaviour in relation to experimental disturbances with a hunting dog, i.e. a moose baying dog (Paper II).

Wildlife and recreational activity

Disturbances by humans often provoke flight reactions: ungulates have been shown to flee from a broad range of activities like hiking, mountain biking, horse riding (Colman *et al.*, 2001; Papouchis *et al.*, 2001; Naylor *et al.*, 2009), snowmobiling (Tyler, 1991; Reimers *et al.*, 2003), cross-country skiing (Cassirer *et al.*, 1992), vehicles (Fortin and Andruskiw, 2003; Naylor *et al.*, 2009), paragliding (Schnidrig-Pretig and Ingold, 2001), helicopters, and fixed-winged aircraft (Frid, 2003). Disturbances that are unpredictable for wildlife are likely to reveal stronger responses than predictable ones. Activity restricted to trails and roads is normally predictable and wildlife can

keep a certain distance according to their comfort zone (Stankowich, 2008). On the other hand, off-trail activities are more unpredictable, and thus may lead to a greater influence zone. For example, mule deer react earlier and move further when disturbed by hiking and mountain biking off-trail activities (Taylor and Knight, 2003).

We expect the evolutionary impact, and thus the biological significance of motor-driven stimuli on wildlife to be negligible as long as wildlife does not experience such disturbance as threatening, i.e. no risk of predation by vehicles. In ungulates, motor-driven stimuli generally generate weaker reactions, though results are inconsistent among species (Stankowich, 2008). Moose has a broad geographical distribution and is a valuable natural resource (Mattsson, 1990). Surprisingly, to my knowledge only one study has compared the impact of different types of human activities specifically in moose and found that motor-driven stimuli provoke weaker response than directly human related ones (Andersen *et al.*, 1991). In contrast, in Plains bison (*Bos bison bison* Linnaeus 1758), wild mountain reindeer (*Rangifer tarandus tarandus* Linnaeus 1758), and elk, motor-driven stimuli were more or as evocative as human-related stimuli (Fortin and Andruskiw, 2003; Reimers *et al.*, 2003; Naylor *et al.*, 2009).

To evaluate the response of non-lethal human activity in a heavily hunted ungulate population, and estimate differences between directly human-related and motor-driven human disturbances, I analyzed moose behaviour to off-trail hiking and snowmobiling activity using a controlled field experiment (Paper III).

Wildlife and infrastructure

Next to short-term recreational and hunting activity, human disturbances can have also a long-term effect on wildlife. In particular, roads are long-lasting ecological footprints of human activity in wildlife habitat (Forman and Alexander, 1998). Road networks increase quickly, and thereby are highly dynamic. For example, in Northern Wisconsin, USA, road density doubled within 60 years, resulting in higher housing density and landscape fragmentation (Hawbaker *et al.*, 2008). Road-effect zones are larger than the physical roads themselves, and for example affect ecologically up to 20 % of the United States, leaving fewer spatial and temporal refuges for wildlife to escape human activity (Forman and Alexander, 1998). Wildlife such as elk can respond to road networks in a nonlinear manner. Thus, the accumulative effects of habitat fragmentation and hunting impact can result

in negative population performance where the population's persistence threshold is passed (Frair *et al.*, 2008). Especially for large mammal species, functionally undisturbed areas seem to be crucial for the populations' well-being (Forman and Alexander, 1998).

Roads fragment continuous habitats and can act as movement barriers (Kuehn *et al.*, 2007), but also facilitate human access into remote areas (Forman and Alexander, 1998). Roads increase wildlife mortality due to wildlife-vehicle collisions as well as by greater predisposition for hunting and poaching (Nielsen *et al.*, 2004; Stedman *et al.*, 2004; Seiler 2005, May *et al.*, 2006). Road effect zones can be large and reduce the effective wildlife habitat size, because animals avoid areas close to roads (Forman and Alexander, 1998; Jaerger *et al.*, 2005; Frair *et al.*, 2008; Theuerkauf and Rouys, 2008; Vistnes, 2008). In contrast to road avoidance, roads can also attract wildlife in response to resource distribution and predation risk. This can lead to roads acting as sinks, and ecological traps concerning both wildlife and road management (Berger, 2007; Laurian *et al.*, 2008; Roever *et al.*, 2008).

In migratory ungulate species, undisturbed migration cycles are essential for populations' persistence, and roads, railroads, fences, or pipelines that act as a barrier might be especially destructive (Bolger *et al.*, 2008). However, the effect of infrastructure is inconsistent, probably due to studies accessing infrastructure impact on different spatiotemporal scales (Vistnes, 2008). Linear infrastructure objects, particular when multiple, increase the risk to act as semi-permeable barriers or to tunnel animals through the landscape, but impact may also differ with wildlife's migratory tradition and environment (Dahle *et al.*, 2008; Vistnes, 2008). The extent of influence zone of anthropogenic structures differs, and can largely reduce the effective area of use, bearing risk for resource depletion in "refuges" (Vistnes, 2008).

Logically, where roads intersect with wildlife passages and movement corridors, risk for wildlife conservation as well as risk for human safety is given, particularly where larger mammal species such as deer (*Cervidae*) are involved (Lavsumund and Sandegren, 1991; Dussault *et al.*, 2007). Road segments differ in their probability to be crossed by wildlife. Probability of an animal to cross a road concerns different spatial scales, and is shaped by individual's movement path, local population behaviour pattern, and at a geographic scale by species life-history traits (Beaudry *et al.*, 2008). At large, the individual movement path is non-random and concerns daily routine,

dispersal, and migration. Movement reflects a decision-making process among behavioural trade-offs and includes individual's internal state and condition (Zollner and Lima, 2005; Nathan *et al.*, 2008), memory ability (Van Moorter *et al.*, 2009), and environmental factors such as landscape structure, resource distribution, and risk of predation (Johnson *et al.*, 2002; Zollner and Lima, 2005; Anderson *et al.*, 2008; Dalziel *et al.*, 2008).

To assess the probability of road-crossings in migratory and solitary-living ungulates on a regional scale, i.e. moose behavioural response to roads, I evaluated the movement behaviour of individual female moose in a daily and seasonal perspective. I related the probability of moose road-crossings to moose movement activity and environmental attributes using GPS location data from free-ranging moose in Coastal, Interior, and Low Alpine areas in Northern Sweden. To access further zones of high risk and to link real wildlife data with wildlife-vehicle collisions records, I evaluated the environmental attributes of road intercepts subject to moose passages as indicated by moose movement data and compared it with sites where moose-vehicle collisions happened (Paper IV).

Objectives

1. To study how moose respond to hunting.
2. To study how moose in a hunted population respond to non-lethal human disturbances.
3. To test experimentally if there is any difference between directly human-related and motor-driven human disturbances.
4. To study how migratory moose respond to roads.
5. To assess when and where is it most risky to be on the roads.

Study area

To meet my thesis objectives I performed my studies on moose ranging in the Coastal, Interior and Low Alpine regions in Northern Sweden, in the Counties of Västerbotten and Norrbotten. The three regions describe a gradient of decreasing human population and road density, but increasing elevation from the east to the west. Moose individuals closer to the mountain region range over larger areas, and migrate on average further distances compared to moose closer to the coastal region (Figure 1; Ericsson *et al.*, 2006; Schön *et al.*, 2007; Bunnefeld *et al.*, unpublished manuscript).

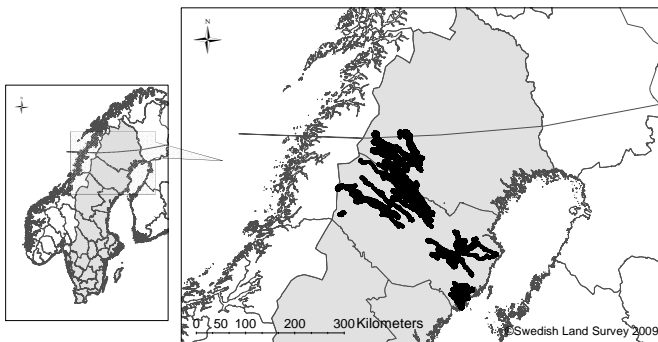


FIGURE 1 Map of Fennoscandia, Sweden in grey. Moose GPS locations in black, located in county Västerbotten and county Norrbotten. The grey line indicates the Arctic Circle.

The Coastal region (63° 42' N 19° 40' E, WGS84) is characterized by relatively high human density (18 persons km⁻², range 2–48; Statistics Sweden, 2009), good accessibility (1.2 km roads km⁻² of which 0.4 km km⁻² are major roads; Swedish Land Survey, 2009), and is comprised of boreal forest with patches of deciduous trees and agricultural activity in a landscape that is flat to gently rolling (95 m, range 0–305 m; Swedish Land Survey, 2009). The Interior (64° 28' N 19° 45' E, WGS84) is dominated by monocultures of Scots Pine (*Pinus sylvestris* Linnaeus 1753) covering a gently rolled landscape with an average elevation of 227 m (range 11–498 m; Swedish Land Survey, 2009). Human density is moderate with an average of 12 persons km⁻² (range 2–48; Statistics Sweden, 2009) and a road density of 1.0 km km⁻² of which 0.3 km were major roads (Swedish Land Survey, 2009). The Low Alpine region (65° 29' N 16° 44' E, WGS84) consists of boreal coniferous and mountainous birch forest, partly above the tree line, with an average elevation of 561 m (range 42–1760 m; Swedish Land Survey, 2009), low human density (1 human km⁻², range 0.2–2; Statistics Sweden, 2009) and low accessibility (0.4 km road km⁻² of which 0.1 km major roads; Swedish Land Survey, 2009).

Throughout Sweden, hunting is the major source of moose mortality, accounting for up to 81% and 91% of mortality in adult female and male moose, respectively, outside wolf territories (Ericsson and Wallin, 2001). Moose populations are managed using an annual quota system. Moose harvest is sustained with a four-month hunting season (Sept-Dec) and annual harvest rates that can come up to one-third of the summer population (Lavsund *et al.*, 2003; Swedish AHWM, 2009). Hunting from any kind of motorized vehicle is illegal (Notisum, 2008). In contrast to the hunting mortality, the mortality risk from natural predators is low, particularly for adult moose. European brown bear (*Ursus arctos* Linnaeus 1758) is present in most parts of the study areas, but predated mostly on moose calves; wolves are absent from the study areas, except a few stray individuals (Swenson *et al.*, 2007; Swedish EPA, 2008).

Paper I and IV include moose location data from the coastal, inland, and low alpine area. Paper II and III provide location data of moose ranging in the inland and low alpine area.

Methods

We immobilized adult moose from a helicopter using a dart gun to inject a mixture of an anaesthetic and a tranquilizer (ethorphine and xylazine; Arnemo *et al.*, 2006). Moose age was estimated by evaluating tooth wear while moose were immobilized (Ericsson and Wallin, 2001). Female moose averaged 6 yrs \pm 0.2 SE and male moose 4 yrs \pm 0.4 SE. Female moose accompanied by offspring were preferentially selected for marking. For the thesis, I utilized data from moose that were equipped with a neck collar that included a Global Positioning System (GPS) receiver, Global System for Mobile communication (GSM) modem, and a traditional VHF-beacon (Vectronic Aerospace GmbH, Berlin, Germany). Positions were calculated at least once per hour and location information was sent to a database server using the GSM cell phone network (Dettki *et al.*, 2004). Using the Short Messaging Service (SMS) of the GSM network nearly real-time tracking was possible by sending the seven latest GPS fixes to the server.

Field methods

Experimental disturbance treatments (Paper II-III)

In paper II the dog handler approached female moose against the wind and let the moose baying dog off the leash at a visible distance of 100–200 m to the moose. Experimental approaches started on the first day of legal moose hunting dog training, 21st of August. To address the effect of reproductive status, half of the females were accompanied by offspring (n=5 individuals) and half without (n=5). To address the effect of repeated disturbance exposure, each moose was approached three times. Moose were on private land, which restricted the timing of our experimental approaches. We used Norwegian elkhounds, which is a common breed to use for moose hunting

in Northern Europe (Thelander, 1992). To track moose and hunting dog interaction, the dog was equipped with a GPS receiver with constant tracking.

In paper III, to simulate recreational disturbances, different moose individuals were approached directly on foot ($n=12$) and on snowmobile ($n=17$), hereafter labelled “hiking” and “snowmobiling”. The approaching person moved in a direct line, as straight as the terrain allowed, and moved at a normal walking pace. The snowmobile approached at a speed less than 20 km h^{-1} . To avoid any additional disturbance of the focal animal, the approaching person returned the way moose had not escaped, preferably returning the same way it came. To address the effect of reproductive status, we included barren females (hiking: $n=5$; snowmobiling: $n=5$) and females accompanied by offspring (hiking: $n=7$; snowmobiling: $n=12$). Snowmobiling activity was conducted during winter and hiking was carried out under snow-free conditions in mid-August. We recorded environmental data and moose behaviour, and for snowmobiling we documented snow condition and the extent to which moose sank in relation to snow depth.

In both II and III, we recorded air temperature, precipitation, wind, and habitat type at the position of moose contact. To assess the perception of risk, we noted moose initial behaviour when approached. The moose individuals approached with a hunting dog had been approached by foot a week before. We expected each individual to be experienced with all stimuli, though to unknown extents.

Statistical analysis

In all four papers I used linear mixed models with moose individuals assigned as random effect to access the variance explained by differences among individuals.

Impact of different hunting activity (Paper I)

For each moose individual ($n=63$), I subdivided the GPS location data into six discrete periods, reflecting different hunting activity and covering a period from mid August to mid October. To access the impact of these different hunting activities on moose behaviour, I analyzed daily moose movement activity [m h^{-1}], movement activity during daytime and nighttime, and moose diurnal activity ranges [km^2].

Experimental hunting disturbances (Paper II)

To access the relative change in moose behaviour when disturbed by a hunting dog, I compared moose movement rates [m h^{-1}] of the hours following disturbance with individual's movement rates during the same hour on the previous day. Thus, I used each individual as its own control and controlled for the potential effects of moose's circadian rhythm. Furthermore, I analyzed moose diurnal activity ranges [km^2] in relation to disturbance and tested for spatial displacement by comparing the overlap and the distance between centroids of moose activity ranges before and after disturbance. To address moose response to repeated disturbance exposure, I compared the relative changes in moose behaviour among three repeated approaches by the hunting dog. Due to spatial inaccessibility, two moose could not be disturbed three times. Out of a total of 28 approaches, at 13 approaches the female was solely accompanied by her own offspring, and at nine approaches the female was observed alone, respectively. For six approaches, the female was not properly seen when disturbed. Apart from the reproductive status, I did not include the accompanying moose status in the analysis. I evaluated the tracking effort of the hunting dog among the repetitions as well as moose initial response towards the approaching dog. To address moose escape behaviour, I analyzed the shape of moose movement path by comparing the linear distance with the cumulative distance moose had moved until resettling, and analyzed the shape of moose escape path in respect to moose, hunting dog, and environmental attributes (Swedish Land Survey, 2008).

Experimental recreational disturbances (Paper III)

To access moose behaviour in response to recreational disturbances, I analyzed moose relative response in respect to movement rates, daily activity ranges as well as their overlap and distance between the centroids before and after treatment, and differences among individuals as in Paper II. For hiking disturbance, out of 12 disturbance trials, four females were solely accompanied by their offspring, four were alone, and four were not properly seen when disturbed. For snowmobiling disturbance, out of 17 disturbance trials, six females were solely together with their offspring, three were alone, and eight were observed in a group when disturbed. Apart from the reproductive status, I did not include the company status in the analysis. I addressed the energetic cost that came along with disturbances by hiking and snowmobiling for adults and potentially following calves. Thus, I calculated the energy expenditures per body mass [$\text{kJ kg}^{-1} \text{h}^{-1}$] using estimates of moose body weight (based on chest circumference, Wallin *et al.*, 1994) and age

(Ericsson and Wallin, 2001). Using these estimates I compared the energetic usage of moose movement rates the first hour following treatment with the same hour on the previous day (Taylor and Heglund, 1982). To determine the factors most influential on moose response, I evaluated the relative changes in moose movement rates in respect to environmental and moose reproductive status and initial behaviour when approached (Swedish Land Survey, 2008).

Moose and infrastructure (Paper IV)

To evaluate the spatiotemporal probability for moose crossing the road over the year, I analyzed GPS location data of female moose ($n=102$) with respect to the road network using 1) major roads only and 2) the entire road network (Swedish Land Survey, 2009). To describe the environmental settings of different road intercepts, I overlaid the entire study area with a 250 x 250 m grid and assigned the percentage contribution of the different vegetation categories, road density, and terrain ruggedness to each grid cell (Riley *et al.*, 1999, Swedish Land Survey, 2009). Moose ranged in Coastal, Interior, or Low Alpine region in Northern Sweden and I classified each moose GPS position to either intersect with a road-crossing event or not. I analyzed the temporal likelihood for moose road-crossings and addressed the spatial distribution by analyzing discrete peaks and dips in probability with respect to moose movement activity and moose distance to the closest road, and environmental attributes. I analyzed the environmental characteristics of the sites at which moose passed the road, evaluated the spatial randomness of such crossing sites, and compared moose road-crossing sites with sites that are object to moose-vehicle collisions.

Results and discussion

Wildlife and hunting activity – large spatiotemporal scale (Paper I)

Different hunting activity may affect species of prey such as moose differently. I evaluated moose movement activity [m h^{-1}] with respect to dog hunting training, hunting of small game and moose. I expected moose in Low Alpine area to be more affected by small game hunting activity, and moose in the Coastal area and in the Interior to be more disturbed by the moose hunt. I predicted disturbed moose would show greater movement activity, greater daily activity ranges and to be more active during nights to compensate for foraging losses.

Low Alpine female moose were on average less active than Coastal and Interior female moose, and male moose (only Low Alpine area) were more active than female moose in any area. Female moose were relatively more active during periods of moose hunt, and showed a trend of lower activity during the temporary break of moose hunt as indicated by corresponding coefficients of variance. In contrast, male moose gradually increased their activity towards the rut, regardless of hunting activity. In respect to the diurnal movement activity pattern, Low Alpine female and male moose were more active during day-time, while diurnal activity did not differ in Coastal and Interior moose. Differences in hunting activity did not have any measurable effect on moose daily activity range in any area or gender.

I concluded that the difference in hunting activity did not affect moose on a larger spatiotemporal level, because I suggested that the observed alterations in individual moose movement activity were not

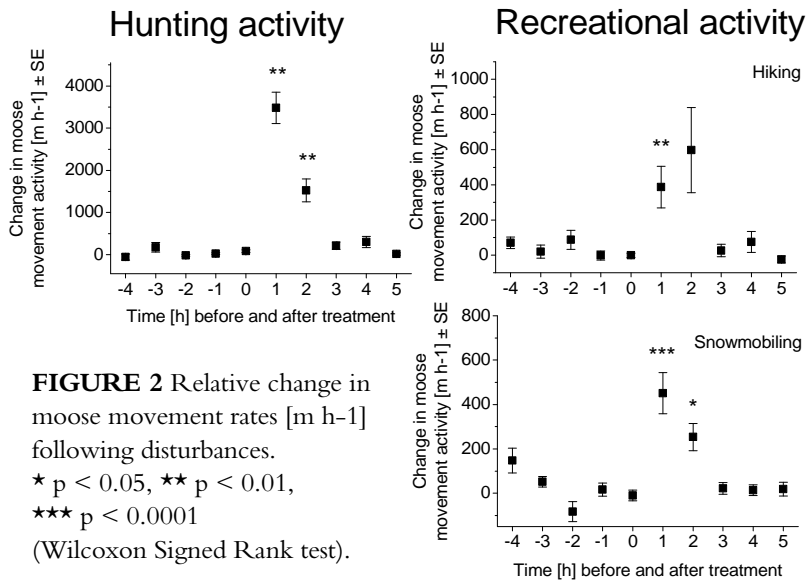
necessarily associated with differences in hunting activity, but likewise may correspond to rutting and foraging behaviour. The analysis of the coefficients of variance indicated large individual variation. For that reason individual-based studies with analysis tools that address variation among individuals are the logical extension of the study.

Wildlife and hunting activity – small spatiotemporal scale (Paper II)

For many ungulate populations, harvest is the dominant source of mortality, which may modify ungulate anti-predator behaviour accordingly. In a controlled field experiment in Northern Sweden, we exposed ten adult female moose to hunting activity using a moose baying dog, studying individual moose behaviour in respect to moose movement activity, daily activity range, and initial response to disturbance.

Moose response was clear, but short-lived with moose being more active during the two hours following disturbance (Figure 2). Enhanced movement activity came along with larger daily activity ranges and disturbance provoked moose to leave the area of disturbance. As a result, daily ranges overlapped less and their centroids were more apart after disturbance than before. The total distance moved by moose until calming down was about twice as much as the linear to the new settle point, which was about 3 km apart from the disturbance position. Instead of fronting which is adult moose natural defence behaviour, we found 80% of the approaches resulted in flight behaviour.

We assume the observed flight behaviour to indicate a modification of moose anti-predator behaviour corresponding to the current (human) dominant top predator. Correspondingly, we suggest that the lengthy period during which human predation dominated and high harvest rates of Scandinavian moose may have resulted in a behavioural adjustment due to selection towards moose being more prone to escape when approached. In turn, this may cause predator facilitation in moose, and may explain the high predation success of wolves on Scandinavian moose due to overlapping predation strategies by humans and wolves.



Wildlife and recreational activity (Paper III)

In wildlife, the disturbance level may differ for different types of human recreational activities. Previous studies are ambiguous about the impact of direct human related and motor-driven stimuli in ungulates. We exposed adult free-ranging female moose experimentally to either off-trail hiking or snowmobiling activity to study individual moose behaviour to these off-trail non-lethal human activities and to evaluate whether moose responded more strongly to direct human-related stimulus (*hiking*) or to motor-driven stimulus (*snowmobiling*).

We found moose responded considerably, but on a short-lived level to both disturbance stimuli. Moose movement rates were elevated for one and two hours following the disturbances with hiking and snowmobiling, respectively (Figure 2). Both disturbance stimuli resulted in moose leaving the area of disturbance. While individuals disturbed by a hiker were eight times as active during the first hour following disturbance as they had been the same hour the previous day, individuals disturbed by snowmobiling were four times as active (Figure 2). About 15 % (*hiking*) and 14 % (*snowmobiling*) of the variance was explained by difference among individuals. We estimated that the observed elevated moose activity would result in comparable increases of energy usage for hiking (16 % and 19 %)

and snowmobiling (19 % and 20 %) disturbance, respectively, in adult moose and calves, respectively.

Aside from considerable change in behaviour, we concluded that the short-lived nature in moose response may indicate negligible effects where human disturbances occur on moderate levels in space and time. However, such disturbances may not be costly for adult moose *per se*, if in good body condition, but need a better understanding of the effects on the body condition of accompanying subadults, especially during severe winter conditions.

Wildlife and infrastructure (Paper IV)

The spatial structure and dynamic nature of infrastructure like roads modifies greatly wildlife habitat, and concerns not only wildlife conservation, but also human safety, particularly when large migratory solitary species like moose are involved. In this study, I evaluated moose behaviour towards roads and I assessed the spatiotemporal probability for migratory adult female moose (n=102) to cross a road in a daily, seasonal, and environmental perspective for Coastal, Interior and Low Alpine areas in Northern Sweden. Moreover, I explored the characteristics of road intercepts being subject to moose road-crossings and moose-vehicle collisions (MVC).

The overall probability for moose cross a road was low. Probability varied largely among seasons and was relatively higher in May and at the end of December and beginning of January, i.e. during periods of moose migration (Figure 3). Moose did not cross roads considerably more often during hunting season. Compared to the seasonal pattern, the daily pattern was weaker. Though, probability for moose crossing a road increased towards the second half of the day in most periods. MVC peaked between mid-October and mid-January winter and most commonly took place at the later afternoon and early evening. About one-third of MVC happened on minor roads. Moose behaviour was an important determinant for the probability of moose crossing a road, with the probability increasing when moose were more active and ranged closer to a road. Difference among individuals contributed differently to the model fit among the periods. Moose that did not cross the road kept on average a larger distance to roads, especially in summer.

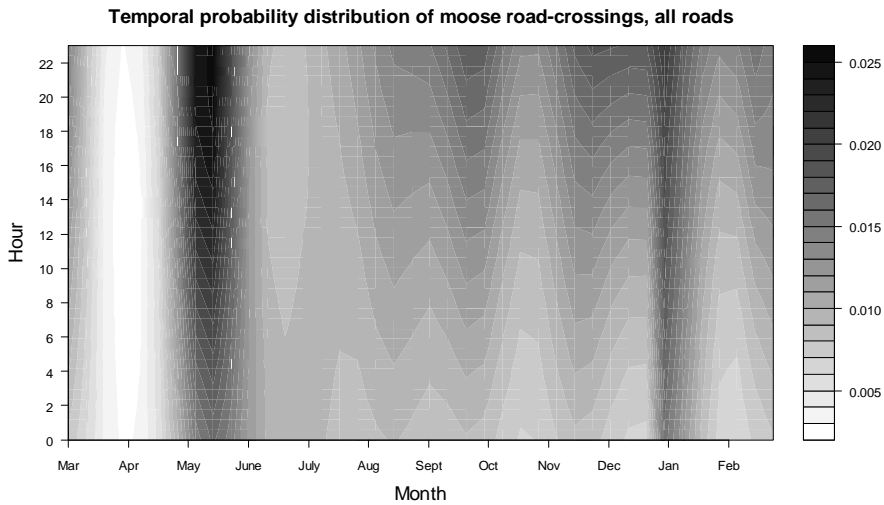


FIGURE 3 Seasonal and daily probability of moose road-crossings (all roads) in Northern Sweden.

Road crossings were spatially aggregated and the probability for moose to cross the road at a certain sites increased with road intercepts having high road density, high proportion of forest, and flat terrain. Sites of moose road crossings and MVC differed with most variance being explained by differences in the abundance of coniferous forest and of urban areas. Most strikingly, MVC were negatively related to coniferous forest abundance, but were positively associated with urban areas (Table 1).

In migratory moose, individual behaviour seemed to strongly affect the movement pattern, being more influential than environmental parameters on the probability for moose crossing the road. Thus, to improve management of wildlife in human-altered landscapes and to sufficiently address conservation and human safety, future analyses need to incorporate individual movement behaviour when predicting movement pattern and space use with respect to large-scale ecological processes.

TABLE 1 Spatial difference between road intercepts subject for moose road-crossings and moose-vehicle collisions (MVC), generalized linear model.

Generalized linear model and hierarchical partitioning
 Difference between road intercepts of moose passages and moose-vehicle collisions

Factor	Variance	Sites of moose-vehicle collisions	Sites of moose road-crossings
Rden ⁻⁻⁻	8 %	326 ± 7.0 m road 250m ⁻²	246 ± 2.0 m road 250m ⁻²
TRI ⁺⁺⁺	3 %	25 ± 0.8	31 ± 0.4
Env.1 ⁻⁻⁻	3 %	4 ± 1.2	-1 ± 0.7
Env.2 ⁺⁺⁺	46 %	-31 ± 1.3	5 ± 0.3
Env.3 ⁻⁻⁻	11 %	8 ± 1.0	-1 ± 0.2
Env.4 ⁻⁻⁻	29 %	16 ± 1.4	-2 ± 0.2

+/- estimate of the factor; ^{++/-} p < 0.01, ^{+++/-} where p < 0.0001

Rden = road density; TRI = terrain ruggedness index; Env.1 = coniferous forest (+), young coniferous forest (-); Env.2 = coniferous forest (+), young coniferous forest (+), mash/open pasture (-); Env.3 = mash/open pasture (+), mire (-), deciduous forest (-); Env.4 = urban area (+), mire (-)

General discussion

Hunting activity affects ungulates such as moose, but the short-term nature of moose response to hunting disturbance complicates the monitoring of hunting impact on a larger spatial and temporal scale (Paper I, II). Hunting disturbance provoked a clear, but short-lived, change in behaviour in moose, and the spatial displacement was small relative to the movement pattern in migratory moose (Paper II; Ball *et al.*, 2001; Ericsson *et al.*, 2006, Schön *et al.*, 2007; Bunnefeld *et al.*, unpublished manuscript). Nevertheless, hunting disturbance caused an abandonment of a site chosen at the first place. Moose are selective browsers, and select hierarchically their habitats with different parameters (e.g. resource distribution, landscape structure, predation risk) being important on different spatial scales (Månsson *et al.*, 2007; Kittle *et al.*, 2008). Consequently, displacement caused by risk of predation or disturbance may lead to a sub-optimal choice of foraging sites, and in the long term may decrease individual body condition, and thereby affecting reproductive performance (Sand, 1996). Beyond that, a re-organization in space may become more complicated in areas of high moose density and high intra- as well as inter-specific competition. Hunting activity affects different moose categories differently (Paper I; Ericsson and Wallin, 1996; Baskin *et al.*, 2004). At large, the short-lived response and short-distance displacement either reflects a well-adjusted response in human-altered moose populations, or may result from a lack of alternative habitats to switch to (Gill *et al.*, 2001).

If the moment of disturbance is unknown, it will be difficult to reveal behavioural responses on larger spatiotemporal scales for wildlife that show short-lived behavioural response when disturbed (Paper I; Cederlund and Kjellander, 1991; Ericsson and Wallin, 1996). Instead, the disturbance impact might be diminished by other activities that affect an animal's movement pattern (Paper I). High stress levels lead to increased faecal

glucocorticoid levels, which can be used to monitor populations' disturbance levels if individual-based analyses are inappropriate and where no disturbance-free refuges are given to track the direct behavioural response to hunting activity (Millsaugh *et al.*, 2000; Creel *et al.*, 2002; Thiel *et al.*, 2008). In particular, in areas where several different types of hunting activities take place, evaluation of the disturbance impact on non-target wildlife might be of interest. For example in systems where multiple deer species co-exist, we need to improve our knowledge to which extent hunting activity targeting one deer species affects other deer species.

Wildlife that do not reduce their responsiveness to hunting disturbance (Paper II), may face a substantial impact on their population performance if disturbance frequency increases. Yet, the degree to which ungulates acclimate to hunting activity varies among species with some species showing a decreasing response when repeatedly exposed to hunting activity (Stankowich, 2008). However, the physical response may not necessarily adequately reflect the physiological stress level. Next, the behavioural response may be accompanied by more sustained physiological consequences (Bateson and Bradshaw, 1997). In ungulates, an individual's body condition largely defines their reproductive success, and this relationship is amplified in harsher climate (Sand, 1996; Ericsson *et al.*, 2001; Mysterud *et al.*, 2005; Bubenik, 2007). In the context of hunting disturbances, infrastructure (e.g. roads) may be especially sensitive, because hunting pressure and road density are closely interrelated (Cooper *et al.*, 2002; Stedman *et al.*, 2004). Depending on the structure and density, road networks fragment continuous habitat, and thereby decrease the dimension of potential refuges, but most notably enable human access into remote areas (Forman and Alexander, 1998). Density of road networks can thereby alter disturbance levels in several dimensions, e.g. hunter density decreases with distance to roads (Stedman *et al.*, 2004) and road density can influence hunting success (Cooper *et al.*, 2002). Consequently, in areas where the road network is dense and high levels of hunting activity occur, ungulates might be more frequently disturbed. Additionally, a dense road network minimizes the quantity of available refuges. This may impair ungulate's overall body condition and thereby may lower populations' reproductive success in the long term.

In adult moose, fronting is the natural defence behaviour that usually fends off an attack by wolves successfully, while moose that run have a high chance of being killed by wolves (Ballard and van Ballenberghe, 2007). In

this thesis, flight was the most common response for moose approached by a hunting dog (Paper II). This behaviour may indicate an alteration in the anti-predator behaviour in Scandinavian moose. When hunted by humans, moose that front the baying dog most likely lower their probability of survival (Thelander, 1992), making running an advantageous alternative strategy where wolves are absent. Little variance among individuals' escape behaviour suggests a uniform response pattern in Scandinavian moose when exposed to hunting activity (Paper II). Tortuosity of the movement path may be an anti-predator behaviour strategy (Fischhoff *et al.*, 2007; Baskin *et al.*, 2004). Tortuous escape behaviour, as an unpredictable escape path, can be advantageous at higher deer densities, because of increased switching frequency among different deer individuals by following hounds (Cederlund and Kjellander, 1991; Ruusila and Pesonen, 2004).

With this thesis I document flight behaviour to be the most common response of moose experimentally exposed to hunting activity (Paper II). Even with the small number of moose individuals in the experiment, the consistency in moose response within and among individuals gives first indications for adjustments in anti-predator response towards a non-native predator. Consequently, if the observed flight behaviour in this study reflects a modification in anti-predator response in Scandinavian moose (Paper II), predator facilitation might occur in areas where wolves and human predation co-exist (Kotler *et al.*, 1992). In Scandinavia, hunting strategies of wolves and humans overlap, possibly resulting in moose behavioural response towards one predator increasing the predation risk by the other (Sand *et al.*, 2006). In ungulates, loss in anti-predator responsiveness can occur within few generations following human-altered predator-prey dynamics (Berger, 1999). However, Scandinavian female moose re-adjust their anti-predator response quickly to reduce neonates predation by brown bears (Berger *et al.*, 2001), but surprisingly, seem to be less well adapted to re-adjust to wolf predation compared to North-American counterparts (Sand *et al.*, 2006). Human predation is still the major source of moose mortality even in wolf territories with moose mortality because of wolf predation accounts for less than 5%, and is only 25-50% of human harvest (Sand *et al.*, 2006). Furthermore, a high moose-to-wolf ratio implies a relative low predation risk for a single moose individual, suggesting a low selection pressure to adjust anti-predator behaviour for wolf predation in Scandinavian moose (Eriksen *et al.*, 2009). In summary, the probability of dying due to wolf attack for individual moose is low, compared with the risk of dying due to hunting. Being beyond the scope of this thesis, future

studies should address the selection force by collecting data about the share of moose shot while standing for the baying dog and while escaping from it, or shot by other types of hunting than with help of a hunting dog. In this context, data about the heredity, i.e. fitness of the focal animal, or the dimension of learning of the behavioural response may be important as well. Moreover, to access the behavioural plasticity as well as the adaptive value of alteration in anti-predator behaviour, the logical extension is the evaluation of the behavioural response of Scandinavian moose to both human and wolves predation in areas where both co-exists.

Compared to non-hunted ungulate populations, hunted ungulates often respond more strongly to human-induced disturbances (Stankowich, 2008). In spite of hunting disturbances being most evocative, lethal and non-lethal human activities provoked comparable overall reactions in moose (Paper II, III). Similar response behaviours suggest a uniform response repertoire in non-naïve animals, but also indicate a comparable risk perception, supporting Frid and Dill's (2002) theory that human-induced disturbances generate analogous behaviour to risk of predation in wildlife. Furthermore, such analogous response behaviour also suggests a more general sensitivity to human proximity in hunted animals. Such effects of human activity on wildlife can result in larger ecological consequences, because human recreational activities often show a high spatiotemporal dynamic and cover a broad range of different activities (Ingold, 2005, Knight and Gutzwiller, 1995). Additionally, the broad extension of infrastructure enables human access into remote areas, and probably will increasingly do so in future (Hawbaker *et al.*, 2008). In particular, directly approaches increase perceived risk in wildlife (Stankowich and Blumstein, 2005). Consequently, human activity that stalks wildlife such as wildlife viewing, tracking and hunting of any kind may increase disturbance levels in wildlife, and needs to be addressed in management actions accordingly.

Unexpectedly, disturbances by hiking and snowmobiling affected moose to a comparable extent, suggesting a similar impact of directly human-related and motor-driven disturbances on moose behaviour (Paper III). However, whereas human-related disturbance provoked a quantitatively stronger response, moose reacted qualitative stronger when disturbed by motor-driven human activity (Paper III). Such similarities in risk perception oppose findings of earlier studies in moose and other ungulate species (Andersen *et al.*, 1996; Stankowich, 2008), though results are inconsistent and can vary among species (Fortin and Andruskiw, 2003;

Reimers *et al.*, 2003; Naylor *et al.*, 2009). Motor-driven human activities are growing in popularity (Fredman and Heberlein, 2003). Such trends may become an increasing problem for wildlife that is sensitive to motor-driven disturbances due to the generally larger area disturbed by motorized activities. Off-trail activities are particularly sensitive, because they result in large influence zones and therefore can lead to a reduction of the effective size of so far undisturbed habitats for wildlife (Taylor and Knight, 2003). The behaviour of the approaching person and subject affects the amplitude of response in ungulates, where more threatening approaches (faster, more direct) cause longer flight distances (Stankowich, 2008). Thus, in areas as well as during periods crucial for wildlife, management needs to provide suitable refuges for wildlife in space and time, but also to inform the public involved in different recreational activities.

In moose, human disturbances lead to increased movement activity that came along with increased energy expenditures, which was comparable for adult and calves (Paper III). However, the estimation of the cost of locomotion in snow is complicated and we expect the relative cost for disturbance by snowmobiling to be higher, especially for smaller bodied individuals such as accompanying calves (Parker *et al.*, 1984; Fancy and White 1985). Although important, comparing disturbances that take place in different seasons is difficult. Individual decision-making may differ with season due to different environmental and individual conditions, and thereby affect risk perceptions and decision rules (Stankowich, 2008). In spite of these aspects, we believe that the evaluation of the relative change in wildlife behaviour to be a good approach to access the relative disturbance character of different human activities. In particular, in areas that are subject of different human activities, we need to assess how different human disturbances affect wildlife, and whether simultaneous activities have additive, cumulative or synergistic impacts on wildlife (Knight and Gutzwiller, 1995; Naylor *et al.*, 2008; Bennett *et al.*, 2009).

Overall though, the short-lived nature of moose behavioural response to hunting and recreational disturbances suggests a negligible impact on moose overall energy budget of single disturbance events (Paper II, III). However, in many cases, wildlife exposed to human-induced disturbances show higher stress levels, as indicated by higher faecal glucocorticoid levels, than their undisturbed counterparts, indicating that the behavioural response may not necessarily tell the whole story (Knight and Gutzwiller, 1995; Creel *et al.*, 2002; Thiel *et al.*, 2008). Stress causes fight-or-flight responses,

resulting in an enhanced state of alertness. However, persistent stress can affect an individual negatively by depleting its body resources. Stress can also affect an individual's biorhythmic by disrupting an individual's conformance with its environment (Berger *et al.*, 2003). At large, the spatiotemporal dynamic of human encroachment into wildlife habitat (Ingold, 2005; Hawbaker *et al.*, 2008), will most likely increase the frequency of human-wildlife interactions in future. This may lead to increased disturbances levels in wildlife and may lead to consequences for populations' fitness in the long term. In ungulates, increased disturbance levels of recreational activities can have direct negative consequences on individuals reproductive success (Phillips and Alldredge, 2000), but may also affect animals indirectly due to the close link between body condition and reproductive success in ungulates (Sand, 1996). All in all, there are good reasons to assume that human activity affects wildlife in a non-linear manner with differences among wildlife species. We need a better understanding and knowledge in different settings to be able to draw conclusions generalized for different species systems and areas subject to different intensities of human activity.

The probability of moose crossing roads varied among seasons and was generally low, but increased when moose migrated (Paper IV; Ericsson *et al.*, 2006; Schön *et al.*, 2007; Bunnefeld *et al.*, unpublished manuscript). In stationary moose, greater road occurrence within moose home range does not necessarily result in individuals crossing roads more often (Laurian *et al.*, 2008). There was no indication that periods of high hunting activity affected the probability of moose crossing roads (Paper IV). Accordingly, increased moose movement activity and spatial displacement following disturbances by hunting activity (Paper II), do not automatically result in more moose crossing roads (Paper IV), and thus not necessarily a higher risk of moose-vehicle collision. These results support findings by Lavsund and Sandegren (1991). In contrast, the risk of moose-vehicle collisions (MVC) seemed to increase with reduction in visual conditions (Paper IV), indicating the influence of driver behaviour, as vehicle speed, on the probability of colliding with a moose (Lavsund and Sandegren, 1991; Seiler, 2005).

Moose crossed roads increasingly during migration, suggesting that permanent, long-term human disturbances such as roads, do not act as strong movement barrier in migratory moose (Paper IV, but see Ball and Dahlgren, 2002). Migratory behaviour and traditional use of migration corridors seemed to be relatively fixed in migratory species, and may not be easily disturbed or altered where disordered by habitat alteration and infrastructure

(Andersen, 1991; Gundersen and Andreassen, 1998; Dahle *et al.*, 2008). Yet the impact of infrastructure on migration behaviour may differ with species, environment, and migration type, and can have devastating consequences on the populations' dynamics in migratory ungulates (Bolger *et al.*, 2008). At large, migratory wildlife that range in a human-altered landscape may be less sensitive to infrastructure, especially solitary-living compared to herds of migratory species (Paper IV; Andersen, 1991; Gundersen and Andreassen, 1998; Bolger *et al.*, 2008; Dahle *et al.*, 2008; Vistnes, 2008), because individual behaviour are important determinants for individuals' movement pattern (Nathan *et al.*, 2008). All in all, evidence indicates that roads lead to lower utilization of habitat in road proximity but not that roads are capable of interrupting wildlife migrations (Knight and Gutzwiller, 1995).

The influence zone of roads generally exceeds the physical size of a road, because wildlife utilize habitats in road vicinity less often (Paper IV; Forman and Alexander, 1998). Such a spatial distribution may suggest that moose perceive habitat in proximity to roads as low-quality habitat (Laurian *et al.*, 2008). However, such perception may differ with season (Paper IV). In ungulates, calving season is a sensitive period and calving grounds may be selected with respect to disturbance or predation (Phillips and Alldredge, 2000; Vistnes, 2008). High road density may restrict the number of undisturbed refuges in an area, and can provide a higher risk of predation and disturbance due to usually higher density of hunters, but also people in general in road proximity (Forman and Alexander, 1998; Stedman *et al.*, 2004). Increasing road networks may gradually increase recreational activities in so far undisturbed areas, disturbing wildlife (Paper II, III; Naylor *et al.*, 2008). In many species, distance to the nearest refuge affects risk perception and animal response towards disturbances (Stankowich and Blumstein, 2005). Compared to North America, most areas in the European landscape offer few refuges unaffected by human activity such as recreation or hunting, giving wildlife less space and time to avoid human disturbances (Ingold, 2005). Extensive road networks seem to affect ungulates like elk negatively and in a non-linear manner, if a threshold in road density is passed (Frair *et al.*, 2008). Especially in large mammals, populations' performance seems to rely much on large undisturbed areas (Forman and Alexander, 1998). Yet, the demand for large continuous areas may differ with species. For example, roe deer populations have increased throughout Europe with the rise of agricultural activity, benefitting from a fragmented landscape, in turn profiting lynx populations (Bunnefeld *et al.*, 2006). Similarly, Scandinavian moose populations benefit from intensified forestry,

especially in winter when they utilized habitats relatively closer to roads, presumably exploiting young coniferous stand in proximity to roads (Paper IV; Ball and Dahlgren, 2002; Lavsund *et al.*, 2003; Månsson, 2007). In summary, the ecological context is an important determinant for wildlife's spatial distribution and risk perception, which need to be considered in corresponding analyses (Brown and Kotler, 2007).

Moose road-crossings were connected with higher movement activity (Paper IV), suggesting that a road crossing is a non-random event in moose (Dussault *et al.*, 2008). Individual behaviour was an important determinant for the probability of moose crossing a road, though the difference among individuals contributed differently to the model fit among the periods (Paper IV). Within movement ecology the impact of individual behaviour on movement pattern has become increasingly acknowledged (Dalziel *et al.*, 2008; Nathan *et al.*, 2008; Van Moorter *et al.*, 2009). In migratory species such as moose, the prediction of pattern in animal movement and space use is a major concern within wildlife management, but also for traffic safety. Road crossings were aggregated (Paper IV), indicating well-established travel routes and corridors in moose, resulting in restricted zones of higher risk for human safety.

Wildlife-vehicle collisions do not necessarily happen where and when ungulates such as moose most commonly crossed roads (Paper IV). The positive relation of moose-vehicle collisions to urban areas and their negative relation to forest opposes findings based on comparisons of wildlife-vehicle collision sites with random sites on road intercepts. As a result and apart from road features, they indicate generally a relative higher risk for traffic safety at road intercepts in proximity to forest cover and abundance, while the relation to urban areas becomes less apparent (Finder *et al.*, 1999; Malo *et al.*, 2004; Seiler, 2005). Such deviations highlight the importance to combine information of wildlife movement with collision data to improve conclusions with respect to wildlife movement corridors and high risk zones for traffic safety (Dussault *et al.*, 2007). Apart from risk and severity of wildlife-vehicle collisions increase with vehicle speed (Lavsund and Sandegren, 1991; Seiler, 2005), about one-third of collisions with moose happened on minor roads (Paper IV). This implies a considerable risk for human safety also on roads with presumed lower vehicle speed, but also perhaps lower safety standards and a lower awareness for collision risk by drivers.

Conclusion and management implications

Humans are an integral part of most ecosystems. Consequently, like any other part of a system, human activity can affect other components in that system.

With this thesis I present data, experimental evidence, and conclusions, which support that human activity such as hunting, hiking, and snowmobiling, affect the movement rates, energy expenditures and spatial distribution of moose in a hunted population.

I show that different human activities provoke comparable short-lived behavioural responses in Scandinavian moose, suggesting a uniform response repertoire towards human activity. While hunting without question provoked the relative strongest response, disturbance perception appeared similar for direct human-related and motor-driven human activity. The similarity in response behaviour indicates a comparable risk perception of different human activities and suggests a sensitivity for human proximity in moose in hunted populations. Such sensibility towards human proximity and different human activities needs to be taken into account in management measures and landscape planning to avoid increasing problems where human activity spreads in space and time and where infrastructure increases access into remote areas, and thereby leaving less undisturbed spatiotemporal refuges for wildlife. Likewise, management needs to consider that different human-induced disturbances that occur simultaneously may have a cumulative effect on wildlife sensitive to human activity.

The short-lived nature of moose response, suggests a negligible effect of single human disturbance events on the overall energy budget of adult

moose. However, an animal's physical response may not tell the whole story, but individual's physiological stress levels may exceed the behavioural reaction. Furthermore, increased movement rates can affect smaller bodied animals such as accompanying calves more strongly, especially during winter. Generally, the short-lived nature of moose response may complicate a monitoring of disturbance impact on wildlife like moose on larger spatiotemporal scales with respect to behavioural responses. Consequently, to satisfy both human demands for recreational activities as well as wildlife well-being, management has to investigate the human impact in a broader context and to apply improved knowledge adaptively to management measures. In this context, to adequately address stress levels in wildlife in areas of high interest for human activities, combining monitoring of populations faecal glucocorticoid levels with individual-based experimental wildlife disturbances may serve as good tools to access the relative impact of different activities on different wildlife species, target and non-target species. For example, management actions may cover the restricted spatiotemporal access of different, but simultaneously occurring, human activities if these affect wildlife cumulatively and where undisturbed refuges are needed.

Hunting, i.e. human predation, can affect wildlife in more than one dimension. With this thesis I give experimental indications for a behavioural adjustment in moose to a non-native predator. The long period during which human predation has dominated and high harvest rates of Scandinavian moose may have driven a selection towards moose being more prone to escape when approached. If such adjustments reflect a modification in anti-predator response, predator facilitation might occur in areas where humans and wolves coexist due to their overlapping predation strategies. To address the adaptive value of the observed behaviour, future studies need to evaluate the behavioural plasticity and the corresponding selection pressure in Scandinavian moose.

With this thesis I document that on large spatiotemporal scale, road crossings are relatively rare events for migratory moose. Frequency of moose crossing the roads varied seasonally and individual moose behaviour contributed largely to the probability for a moose crossing a road. Sites at which moose crossed the road were aggregated, suggesting well established travel routes and corridors in moose. Apart from when crossing a road, moose showed a low utilization of habitats in road proximity. Consequently, to access animal movement patterns properly, analyses require the consideration of individual behaviours to correctly predict movement

behaviour such as habitat utilization, travel routes and corridors, and risk zones for traffic safety.

Furthermore, with this thesis I show that moose-vehicle collisions do not necessarily happen where and when moose most commonly cross roads, but suggest a higher risk for human safety during times of reduced visibility and in proximity of human settlements. My work indicates that information of wildlife movement should be combined with collision data to improve conclusions with respect to wildlife movement corridors and high risk zones for traffic safety.

Future perspectives

To specifically address the ecological consequences of the dynamic nature of human intrusion into wildlife habitat, we need to improve our understanding not only of the direct impact of human activity such as hunting, recreational activity and infrastructure on wildlife populations, but also of the indirect impact. While the direct effects usually concern wildlife's immediate response, the indirect effects involve potential additive or synergistic impacts (Knight and Gutzwiller, 1995). Still, little is known about the cumulative impacts of different human activities and their disturbance thresholds in different wildlife species.

Better knowledge is especially needed in systems where humans account for the major source of wildlife mortality, i.e. functionally belong to the guild of top predators, because here human activity may affect wildlife in more than one dimension. The dynamics of natural predator-prey systems are largely affected by the indirect, non-consumptive, effects of predation risk (Creel and Christianson, 2007). To properly evaluate the role of the effects of predators on prey population and community dynamics, predator-prey interaction models should incorporate prey behaviour and other predator-induced traits (Peckarsky *et al.*, 2008). Apart from addressing the demographic side effects (Milner *et al.*, 2007), today's research is still in its infancy regarding the non-consumptive effects of human predation on prey-predator systems. Given indirect effects of human predation, we surely need to improve our understanding about the evolutionary impact on animal anti-predator behaviour in response to human predation in the long-term (e.g. individuals' body condition, physiological stress levels, populations' performance) as well as the impact when natural predators re-colonize.

In particular, European wildlife has experienced major modifications of their environment due to human activity over the last 100–300 years, ranging from habitat degradation and minimization, as well as profound changes in the species structure of ecosystems. In respect to ungulates, many prey–predator systems have been degraded from multiple predator systems to single predator systems in which human harvest dominates ungulate mortality. Based on animal behaviour theory, a corresponding modification in the anti-predator behaviour of affected populations seems reasonable, and should be better investigated. This is certainly important in systems where natural top predators re-colonize, which potentially results in novel trade-off situations for the prey species in respect to minimize their risk of predation. In this context, individual-based analyses are particularly valuable. Their ability to account for behavioural differences among individuals gives an option to address differences in individual's experience background and responsiveness to different procedures, stress levels as well as different environments.

Much of previous research concerns case studies and snap-shots of wildlife–human interactions. To live up to today's dynamic development of human activity as well as future development with respect to consequences that may come along with climate change, future wildlife ecology research needs to incorporate human dimension on broader scales in space and time. Many human activities take place on landscape scale just as wildlife covers broad spatial scales. Thus, future research concerning human–wildlife interactions has to include landscape ecology, but also political and socio-economical aspects. Besides their ecological frame, for most species their distribution and persistence is a political question (Ericsson and Heberlein, 2003; Lavsund *et al.*, 2003; Ericsson *et al.*, 2008). Socio-economic aspects influence human actions, public attitudes, and environmental development. In turn, they affect also wildlife environment, wildlife population dynamics, and conservation as well as research effort (Martín-López *et al.*, 2009). From a natural resource point of view, wildlife is a significant and valuable resource, concerning different human interest groups, which challenges management and conservation. Proceeding industrialization may alter hunting attitudes and interest as well as hunter numbers, and popularity of different recreational activities may also change over time (Heberlein *et al.*, 2002; Fredman and Heberlein, 2003). Thus, aside from basic research to improve our understanding of underlying processes, future research needs to strengthen the applied and interdisciplinary approaches that include the dynamic nature of the human dimension into wildlife environment. These

aspects we need to include adequately when modelling future developments under different management scenarios (Bennet *et al.*, 2009). Along with climate change, we expect changes in landscape structure and arrangement, and thus, different use and spatial distribution of humans. Many wildlife species range over relatively large areas, ignoring national and regional administrative borders. Nevertheless, much research still focuses on single, separated systems, restricted by administrative borders that may differ in their socio-economical background as well as management system. Ignoring natural wildlife ranges and borders limits the quality of predictions of future wildlife population dynamics and development.

Human and wildlife interact and do share time and space – we have to improve our knowledge and understanding about the ecological consequences on both levels.

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Swedish summary - Svensk sammanfattning

Älgars beteende och mänsklig aktivitet

Människan tar en allt större plats i vilda djurs levnadsmiljö. Vår aktivitet kan både direkt och indirekt påverka ett djur, liksom hela dynamiken i ekosystemet som djuren finns i. Vi har fortfarande en begränsad kunskap om beteendet hos vilda däggdjur och fåglar (vilt) i ett landskap med mänsklig påverkan, särskilt där jakt inverkar på deras överlevnad. Infrastruktur som vägar lämnar dessutom långvariga fotspår i viltets habitat som de måste anpassa sig till. Avhandlingen behandlar beskrivande och experimentellt hur älgar i norra Sverige reagerar på mänsklig aktivitet som jakt och friluftsliv (turism), samt hur de reagerar på infrastrukturstörningar som vägar. Älgen är ett lämpligt modelldjur för att studera detta eftersom den har samexisterat med människan under lång tid och jakt är dess dominerande dödsorsak.

Påverkan från jakt och friluftsliv ökade älgens rörelseaktivitet momentant och ledde till att djuren bytte område. Älgens reaktionsmönster i experimenten tyder på en genomgående likformig respons till oförutsedda störningar. Direkt jaktlig störning av individuella älgar orsakade den kraftigaste reaktionen. Vid jaktstörningsexperimenten flydde oftast älgarna direkt när de spårades upp av en lösspringande älghund. Det tyder på att älgarna kan ha anpassat sitt försvarsbeteende till en mänsklig predator. Jakt med löshund och vargens sätt att jaga älg liknar varandra, men älgens optimala försvarsbeteende vid jakt av den ena eller andra skiljer sig. Därmed kan beteendet att fly vid jakt med löshund öka älgens risk att tas av rovdjur som vargar. Älgarna reagerade likartat på övriga experimentella störningar - rörlig friluftsliv (människa) och direkt störning med snöskoter. Trots den i

vissa fall kraftiga reaktionen omedelbart efter en enstaka störning, visar mina beräkningar att den troligen bara har en minimal påverkan på älgens totala energibudget.

I Norrland passerade älgarna vägar relativt sällan. De flesta vägpassagerna skedde under älgens vandring i maj, samt i slutet av december och början av januari. Under vandringen passerade älgarna vägarna dygnet runt. Däremot ökade risken för en älgolycka med sämre ljusförhållanden under dygnet och året. Förutom när en älg passerade en väg, rörde sig älgarna i liten utsträckning i vägnära områden, framförallt var det tydligt under sommaren. Det indikerar ett lägre utnyttjande av vägnära miljöer än förväntat. Vägpassagerna var koncentrerade till ett fåtal vägsträckor som tyder på väl etablerade vandringskorridorer. Sannolikheten för en älg att passera en väg var högre där vägnätet var tätare, där det fanns mycket skog och där terrängen var plan. Ett oväntat resultat var att huvuddelen av älgolyckorna inträffade nära mänsklig bebyggelse och inte nödvändigtvis där älgarna oftast passerade vägarna. Sannolikheten för vägpassager var inte avsevärd högre under älgjakten jämfört med övrig tid på hösten. Det tyder på att älgens ökade rörelseaktivitet och förflyttning som följer av en jaktstörning inte automatiskt resulterar i att älgar passerar vägar oftare. Slutsatsen är att älgjakten inte ökar risken för älgolyckor i norra Sverige. Noterbart är att en tredjedel av älgolyckorna inträffade på mindre vägar som troligen har lägre säkerhetsstandard och där förarens riskmedvetenhet troligen är lägre.

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